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BREEDING BIOLOGY OF PROTHONOTARY WARBLERS IN RIVERINE HABITAT IN TENNESSEE

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ABSTRACT.—The breeding biology of Prothonotary Warblers (*Protonotaria citrea*) was studied in the center of their summer range along the Tennessee River in west central Tennessee in 1985 and 1987. Data were collected on clutch and brood sizes, numbers of young fledged, fledging weights, incidences of predation, cowbird parasitism, and nest abandonment for birds nesting in nest boxes. Warblers in this study had relatively high reproductive success compared to populations studied by Walkinshaw (1941) in Tennessee and Michigan. Prothonotary Warbler clutch sizes, brood sizes, and numbers fledged were significantly smaller in the second half of the season than in the first half. However, fledging success (number fledged/number eggs laid) was similar in both early and late nests. Prothonotary Warblers suffered 7.1% (of 831 eggs) hatching failure due to egg infertility or embryo death. Nestling mortality not due to predation or abandonment was low (2.6% of 700 nestlings), occurring mostly in broods where hatching was asynchronous. Frequency of predation was relatively low (20.9% of 191 nests) compared to Walkinshaw's (1938) results. However, although no cowbird parasitism was observed in 1987, parasitism in 1985 was much higher (20.3% of 128 nests) than that reported by Walkinshaw (1938). *Received 10 May 1988, accepted 11 Oct. 1988.*

Little has been published on breeding biology of Prothonotary Warblers (*Protonotaria citrea*) in the past 40 years. Walkinshaw (1938, 1939, 1941, 1953) intermittently collected data on nest initiation dates, clutch sizes, and life histories in southern Michigan. The population he studied was fairly small (11–14 pairs), perhaps because it was near the edge of the breeding range for the species. Walkinshaw (1941) also compared data gathered on Prothonotary Warblers in Michigan to data from a population in northwestern Tennessee. Some differences in nesting behavior were found between the two populations, although relatively fewer data on ecology of the warblers in Tennessee were obtained. Only two other studies of Prothonotary Warbler breeding biology, other than anecdotal reports, have been published during this century. Meyer and Nevius (1943) studied only four nests, and Kleen (1973) considered only territory sizes and return rates of the warblers.

It is important to gather more quantitative data on breeding biology of this species for two reasons: (1) the Prothonotary Warbler is unique because it is one of only two cavity-nesting wood-warblers (Parulinae). Data

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on Prothonotary Warblers can be compared with data from other, more intensely studied cavity nesters from different families and at different latitudes (e.g., Pied Flycatchers [*Ficedula hypoleuca*], parids [*Parus* spp.], bluebirds [*Sialia* spp.], and various wrens). (2) Prothonotary Warblers require swampy or riparian habitat for nesting and populations may be declining in northern states due to loss of suitable swampy habitats (Graber et al. 1983; but see Robbins et al. 1986). This species breeds in relatively large numbers in southern states, but even in those areas, wetland and bottomland hardwood habitats are disappearing at an alarming rate (less than 25% of the original bottomland forest in the southeastern United States exists today; Harris et al. 1984).

Here I present quantitative information on the breeding ecology of Prothonotary Warblers nesting in riverine habitat within the center of their breeding range.

STUDY AREA AND METHODS

Field work was conducted from 5 April to 17 July 1985 and from 4 April to 20 July 1987, along the Tennessee River in Benton County, Tennessee. The study area extended approximately 25 km along an impounded section of the river (Kentucky Lake). In this area the width of the river ranges from approximately 1 to 3 km. During summer months the river level is raised, due to damming, flooding vegetation along the shores and creating 1–5-ha islands. The river is bordered by hilly, oak-hickory forests. Riparian habitat occurs in narrow strips (usually less than 50 m in width) along the shores and is dominated by willows (*Salix* spp.), buttonbush (*Cephalanthus occidentalis*), sweetgum (*Liquidambar styraciflua*), red maple (*Acer rubrum*), hackberry (*Celtis occidentalis*), river birch (*Betula nigra*), and American elm (*Ulmus americana*).

In 1985 and 1987, I placed a total of 426 milk carton nest boxes (Fleming and Petit 1986) on trees along shores and on islands (1985 only) within the river at heights of 1.5–2.0 m. Because Prothonotary Warblers usually require standing water in the breeding habitat (Petit et al., unpubl. data), nest boxes were arranged in a linear fashion parallel to the river and were placed over water approximately 5–15 m inland from the outer edge of the vegetation. Boxes were erected in late March to early April before the return of the warblers to their breeding grounds.

Territories of color-banded males were mapped intensively only in 1985 and were based on observations of locations of singing posts and aggression between males over a period of 30–40 days. In some cases, a male's response to a playback of song was used in determining boundaries. Nest boxes were checked once every 7–10 days for the presence of nests. Once nests were found, they were checked an average of 2–3 times per week. For each nest, I recorded clutch size, brood size, and number of young fledged. Clutch size was number of eggs incubated by the female, and brood size was number of young that hatched, if known, or number of nestlings present in the nest. Adult Prothonotary Warblers usually do not remove unhatched eggs from the nest (pers. obs.). This aided in determining how many young had hatched successfully and, in many cases, the cause of hatch failure (e.g., embryo death, egg infertility). Lengths and widths of eggs were measured to the nearest 0.1 mm with dial calipers. Number of young successfully fledged was the number of young present in the nest at 9 or 10 days after hatching. I weighed nestlings at 9 days, when possible, to avoid causing premature fledging. Weights were obtained to the nearest 0.1 g using a 50-g Pesola

scale. Analyses of nest success included only nests in nest boxes which I monitored from incubation through termination. Nests in natural cavities and nests of birds in polygynous matings (unpubl. data) also were not included in analyses. Because there were no statistical differences in clutch and brood sizes and numbers of young fledged between years (Mann-Whitney *U*-tests, $P > 0.10$), data from both years were pooled for analyses. For analyses of nest success over time, nesting attempts were categorized as early or late according to distributions of nest initiation dates in each year.

Incidences of predation, nest abandonment, and Brown-headed Cowbird (*Molothrus ater*) parasitism were also noted. Predation was assumed to have occurred if nest contents were prematurely absent. The type of predator was determined according to whether the nest was disturbed (mammalian) or not (snake) (Best 1978).

RESULTS

Dates of arrival and territory establishment.—In both 1985 and 1987, male Prothonotary Warblers were first seen on study sites between 8 and 11 April, and females were seen about a week later. Within the first several days after their arrival, males explored nest boxes and natural cavities, usually without singing. Males established territories around one or several nest boxes/cavities and increased singing rates usually to 4–6 songs per minute, although this rate varied with time of day (unpubl. data). Small amounts of moss usually were placed by the male into each nest box within his territory. Occasionally, males placed up to 7.5 cm of moss within one box, fashioning a nest depression by sitting down in the moss much like an incubating female. Territorial behavior included vigorous displays toward and attacks on neighboring males, which often involved long chases and some actual contact between birds. Territory sizes in 1985 ranged from 0.1 ha to 1.2 ha ($\bar{x} = 0.48 \pm 0.23$ [SD] ha; N = 80).

Upon their arrival, females inspected cavities or nest boxes, and once a cavity was chosen, they filled that cavity nearly to the entrance hole with moss. Then they constructed a nest lining from rootlets, bark strips, and grape (*Vitis* spp.) vine. Colored fishing line also was used in construction of nearly all nests.

Nest initiation and clutch sizes.—Data were collected from 265 Prothonotary Warbler nests, including 27 nests in natural cavities. Most of the latter were in abandoned Downy Woodpecker (*Picoides pubescens*) cavities; one was in an abandoned Red-winged Blackbird (*Agelaius phoeniceus*) nest (Petit and Petit 1988). The first nest was initiated (first egg laid) on 23 April and 1 May in 1985 and 1987, respectively. Mean initiation date for early nests (initiated prior to 22 May and 30 May in 1985 and 1987, respectively) was significantly later in 1987 ($\bar{x}$ date = 10 May) than in 1985 ($\bar{x}$ date = 3 May; Mann-Whitney *U*-test, $Z = 5.02$, $P < 0.0001$). In both years, most females laid two clutches, resulting in bimodal distributions of clutch initiation dates (Fig. 1). Of the 66 females which were known to make at least two nesting attempts, 51 (77%) at-

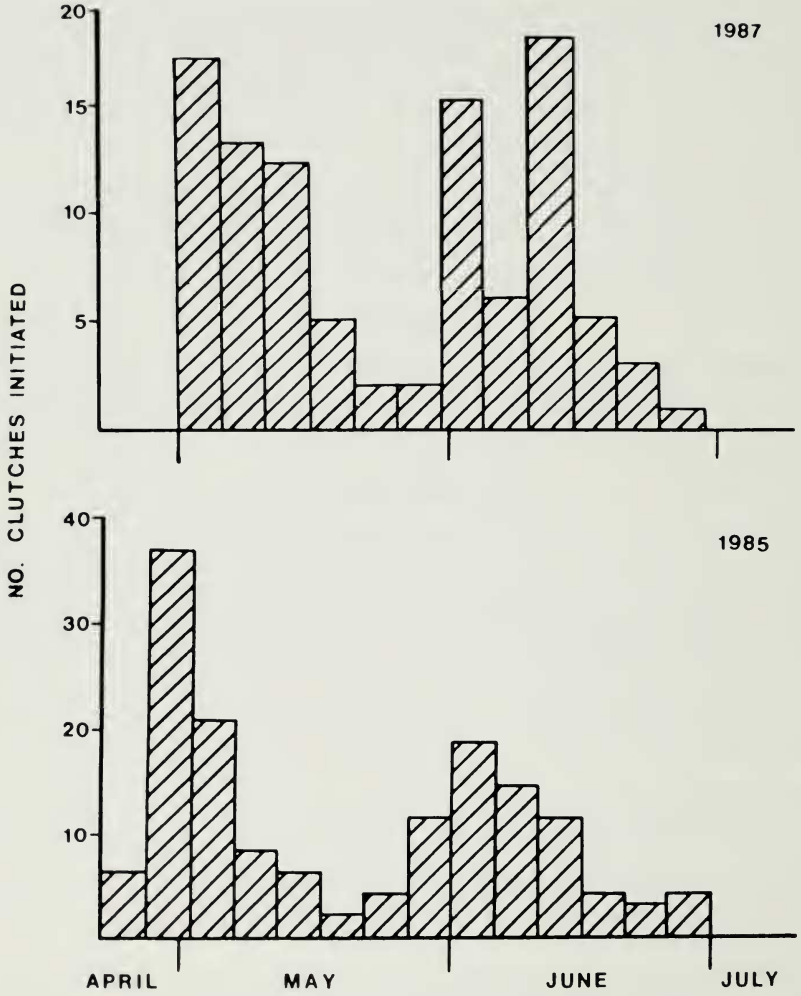

FIG. 1. Distributions of Prothonotary Warbler clutch initiations (first egg laid) per week in west central Tennessee during 1985 and 1987.

tempted a second clutch after a successful nesting attempt (at least one young fledged), and 36 (55%) were successful in both nesting attempts. No female was observed to attempt a third nest after two successes. Mean initiation dates for late nests (initiated after 22 May 1985 or 30 May 1987) were 7 June in 1985 and 13 June in 1987 (Mann-Whitney *U*-test; $Z = 2.26$, $P = 0.024$). An overall average of 4.73 ± 0.65 [SD] eggs ($N = 123$ nests) were laid per nest, and incubation lasted approximately 12 days

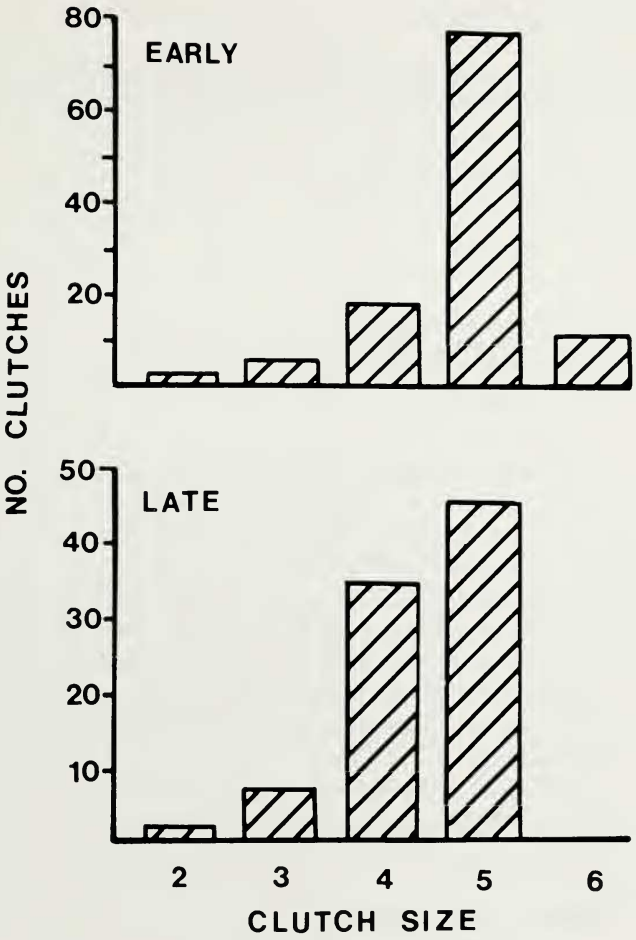

FIG. 2. Distributions of Prothonotary Warbler clutch sizes in early (initiated on or before 22 May 1985 or 30 May 1987) and late (initiated after 22 May 1985 or 30 May 1987) nests. Early clutches were significantly larger than late clutches.

and began when the penultimate egg was laid. Prothonotary Warbler eggs had a mean length of 17.68 ± 0.64 [SD] mm and a mean width of 14.30 ± 0.51 mm (N = 512). In both early and late nests, the most common clutch size was 5 (Fig. 2).

Comparisons of early and late nests.—Comparisons between early and late nests included only nests for which data were complete (i.e., all parameters were known) and which did not suffer predation, cowbird parasitism, or abandonment. Clutch sizes, brood sizes, and numbers of young

TABLE 1

PROTHONOTARY WARBLER CLUTCH SIZES, BROOD SIZES, NUMBERS OF YOUNG FLEDGED, AND FLEDGING WEIGHTS IN EARLY AND LATE[a] NESTS

	Early		Late		
	N	$\bar{x}$ (SD)	N	$\bar{x}$ (SD)	P^b
Clutch size	65	4.95 (0.54)	55	4.56 (0.56)	0.0005
Brood size	65	4.47 (1.01)	55	4.16 (0.82)	0.04
Number fledged	65	4.43 (1.03)	55	3.98 (0.97)	0.01
Fledging weight (g)	120	11.71 (0.71)	79	11.51 (0.93)	0.14

[a] Early nests = initiated on or before 22 May 1985 or 30 May 1987, Late nests = initiated after 22 May 1985 or 30 May 1987. Nests suffering predation, cowbird parasitism, or abandonment were excluded from these analyses. Data were combined for 1985 and 1987.

[b] Mann-Whitney *U*-tests, two-tailed.

fledged were significantly greater in early nests (N = 65) than in late nests (N = 55; Table 1). However, mean fledging success (number fledged/number eggs laid) was similar for both early (89%) and late (87%) nests (Mann-Whitney *U*-test; $Z = 0.77$, $P = 0.44$).

Overall hatching and fledging success.—Of 831 eggs laid, 700 (84.2%) hatched and 620 (74.6%) young fledged. Fifteen (1.8%) eggs were known to have suffered embryo death, and 11 (1.3%) were infertile. Twenty-four (2.9%) other eggs failed to hatch for one of these two reasons, but actual causes of failure were not determined. The remainder were lost to predation or abandonment.

Two Prothonotary Warbler young apparently died in the process of hatching. Sixteen (2.3%) nestlings died either from starvation or apparent trampling by larger nestmates. Five of those nestlings were in broods where hatching was asynchronous and in which the last egg hatched 12 to 24 hours after the penultimate egg hatched. The remaining nestling mortality was due to predation or nest abandonment.

Predation, cowbird parasitism, and nest abandonment.—Predation occurred in 20.9% of all Prothonotary Warbler nests (Table 2) and occurred more often on nestlings than on eggs. Although overall predation rates were significantly different in 1985 and 1987 (16.9% vs 29.5%; $G = 3.82$, $P = 0.051$), when nests were separated into early and late, predation rates were not different between years (Table 2). Nests were apparently depredated by snakes and mammals (mostly raccoons [*Procyon lotor*], whose prints have been visible on and around depredated nest boxes). Frequency of predation did not differ between early and late nests (1985 and 1987 combined; Table 2). In 1985, predation occurred in similar proportions on island (11 of 78 nests) and mainland (11 of 82 nests) plots ($G = 0.01$, $P > 0.50$).

TABLE 2

FREQUENCIES OF PREDATION, COWBIRD PARASITISM, AND NEST ABANDONMENT IN EARLY AND LATE[a] PROTHONOTARY WARBLER NESTS IN 1985 AND 1987

Number of nests	1985		1987	
	Early	Late	Early	Late
Total	77	53	37	24
Depredated (%)[b]	14 (18.2)	8 (15.1)	12 (32.4)	6 (25.0)
Parasitized (%)[c]	19 (24.7)[d]	7 (13.2)[e]	0	0
Abandoned (%)	6 (7.8)	2 (3.8)	1 (2.7)	1 (4.2)

[a] Early nests = initiated on or before 22 May 1985 or 30 May 1987, Late nests = initiated after 22 May 1985 or 30 May 1987.

[b] Significant difference between overall (early and late) predation rates in 1985 and 1987; $G = 3.82$, $P = 0.051$.

[c] Significant difference between overall (early and late) parasitism rates in 1985 (N = 128) and 1987 (N = 59); $G = 21.60$, $P < 0.0001$.

[d] Significant difference between parasitism rates in early nests in 1985 (N = 75) and 1987 (N = 35); $G = 16.35$, $P < 0.0001$).

[e] Significant difference between parasitism rates in late nests in 1985 and 1987; $G = 5.54$, $P = 0.02$.

Twenty-six (20.3%) Prothonotary Warbler nests were brood parasitized by Brown-headed Cowbirds in 1985, and although early nests were parasitized more frequently than late nests, the difference was not statistically significant ($G = 2.94$, $P = 0.09$; Table 2). No brood parasitism occurred in nests in 1987. Data on effects of cowbird parasitism on warbler reproductive success will be published elsewhere.

Female Prothonotary Warblers abandoned 10 (5.2%) of 191 nests, and abandonment rates did not differ between years ($G = 0.75$, $P = 0.39$) or between early and late nests (Table 2). Two (20%) of the 10 nests were abandoned after young had hatched. Based on timing of abandonments, none was attributable to observer disturbance.

Fledging weights.—Prothonotary Warbler young fledged 10–11 days after hatching, and overall mean weights at 9 days were 11.71 ± 0.71 g and 11.51 ± 0.93 g from early and late nests, respectively. Weights of fledglings from early nests in 1985 were nearly significantly greater than those from early nests in 1987 ($Z = 0.732$, $P = 0.058$). However, weights did not differ between years for fledglings from late nests. Whether years were analyzed separately or together, mean fledging weights did not differ significantly between early and late nests (Table 1).

DISCUSSION

Dates of arrival and territory sizes.—Because most of the information on Prothonotary Warblers comes from Walkinshaw's (1938, 1939, 1941, 1953) studies, I compare my data primarily with those from his Michigan and Tennessee populations. The time of arrival for male Prothonotary

Warblers on my study area falls approximately one month earlier than in Walkinshaw's (1938) Michigan study and 1–2 weeks later than for males on Walkinshaw's (1941) Tennessee study site (based on date of first egg laid). The reason for the discrepancy between arrival dates in this study and in Walkinshaw's Tennessee study is not clear, but it simply may reflect normal yearly variation.

Mean territory size for 13 Prothonotary Warbler pairs in Michigan (Walkinshaw 1953) was 1.48 ha, nearly three times larger than the mean territory size in my study. Manipulation of nest-box density (Petit 1986) in my study may account for this difference. (Results of those manipulations will be published elsewhere.) However, even on plots where no nest boxes were present, territory size averaged only 0.64 ± 0.10 ha (SD) (N = 10). On the other hand, Kleen (1973) found that the average size of 10 Prothonotary Warbler territories in southern Illinois was approximately 0.50 ha, similar to the average territory size in this study. All of the birds in Kleen's (1973) study defended territories around natural cavities. Differences in territory size may also be due to differences in habitat quality in the different studies. Walkinshaw (1953) studied Prothonotary Warblers nesting in bottomland habitat bordering a fairly small river (Battle Creek River, Michigan). Kleen (1973) and this study dealt with warblers nesting in flooded habitat where there probably were more nest cavities (dead snags) available and where nearly all nests were situated over standing water.

Variation in clutch sizes and reproductive success.—Average clutch size and incubation time in this study were similar to those for Walkinshaw's (1941) Tennessee population, and as in Walkinshaw's study, clutch size decreased during the season. In both Walkinshaw's Tennessee population and this study, mean clutch sizes were smaller than those of Michigan warblers, particularly early in the season. Egg measurements in the present study were similar to those for Walkinshaw's (1941) Tennessee population ($\bar{x}$ = 17.88 × 14.29 mm, N = 98) and were smaller than warbler eggs in Michigan ($\bar{x}$ = 18.53 × 14.70 mm, N = 196; Walkinshaw 1941). Although warblers in Michigan (Walkinshaw 1941) often attempted a second nesting after the first was successful (at least one young fledged), none of the breeding pairs had two successful nests. In Tennessee, Walkinshaw (1941) found that two broods often were raised in one season, although he did not document exact percentages. More than three-quarters of the females in this study made at least two nesting attempts during the season, and a large percentage of those were successful in both nesting attempts. Differences in clutch sizes and tendency to double-brood in the different areas may be a consequence of differences in lengths of breeding seasons at the different latitudes (Lack 1947, 1948). For instance, Walkinshaw

(1941) reported the average breeding season (from date of first egg laid to date of termination of last nest) of Prothonotary Warblers in Michigan was 53 days compared with 108 days of nesting in Tennessee.

Hatching and fledging success.—Prothonotary Warblers in this study had high hatching success (84.2%) and low nestling mortality (11.4%), including losses due to predation and nest abandonment. Walkinshaw (1941) found hatching success of 38% of 413 eggs laid in Michigan, and 61% of 163 eggs laid in Tennessee. Nestling mortality was 33% in Michigan, but no nestling mortality occurred at his Tennessee area. Walkinshaw (1941) attributed the lower nesting success in Michigan to competition from and nest destruction by House Wrens (*Troglodytes aedon*) which were not present in either Tennessee site. Similarly, preliminary data from an Ohio population of Prothonotary Warblers (K. E. Petit 1988, Petit et al., unpubl. data) suggest that House Wrens may have an adverse effect on warbler nesting success there.

Much of the nestling mortality not due to predation or abandonment occurred in nests where hatching was asynchronous. In those nests, the nestlings that hatched last were apparently at a disadvantage compared with their older, larger nestmates, and, at least in some cases, the youngest nestling was the one to die.

Predation, cowbird parasitism, and nest abandonment.—Although predation increased in frequency from 1985 to 1987, the percentage of nests depredated in this study was lower than in Walkinshaw's (1941) study, where at least 41% of 27 Prothonotary Warbler nests suffered predation. By placing their nests over water, Prothonotary Warblers may be better protected from mammalian predators. In Ohio, Prothonotary Warblers nesting over fairly deep (30–50 cm) water within a marsh suffered no predation, whereas House Wrens nesting over land in the same marsh and the same nest box type suffered 20% predation by mammals (K. E. Petit 1988). As might be expected, most of the predation in the present study was on nestlings rather than on eggs, perhaps due to increased activity around the nest site (e.g., Best 1978). Predation frequency did not vary with time of the season, and nests on island plots were not safe from predation. This last result perhaps is not surprising because the majority of nests apparently were destroyed by snakes. Raccoons also were present on some island plots.

In Walkinshaw's (1938) study, cowbirds parasitized only 3 (10.7%) of 28 Prothonotary Warbler nests in Michigan. Warblers in this study suffered more than twice as much brood parasitism in 1985, but none in 1987. Differences in parasitism rates in Walkinshaw's and my study simply may reflect annual variation in regional or local densities of cowbirds.

Fledging weights.—Fledging age for Prothonotary Warblers in this study

was similar to those in Walkinshaw's (1941) Michigan (11 days) and Tennessee (10.75 days) populations. Walkinshaw did not report fledging weights for his Tennessee birds, and in Michigan mean weight of 10 birds at 9 days was 12.41 g (Walkinshaw 1938, 1939). Meyer and Nevius (1943) reported mean 9-day weight of 11.82 g (N = 12) for Prothonotary Warbler young in eastern Tennessee. Whether those differences between studies are real, and reflective of geographic variation in weights, or the result of sampling error is not known. However, because Michigan birds laid larger eggs than Tennessee birds (Walkinshaw 1941, this study), it is probable that nestlings were also larger (and consequently weighed more) in that northern population. A positive correlation between egg size and nestling size has been found for some other passerine species (e.g., Howe 1976, Richter 1984).

Prothonotary Warblers in this study had relatively high nesting success, certainly higher than that reported for a population in Michigan (Walkinshaw 1941). Although predation had the greatest effect on warbler reproductive success, relatively fewer nests were lost to predation in this study than in Walkinshaw's Michigan population. The high reproductive success in this study is probably due to a longer nesting period, compared to that in Michigan, and a lack of competition for nest-sites with other, more aggressive species (i.e., House Wrens).

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